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An Analysis of Reproductive Behavior in the Mouthbreeding Cichlid Fish, *Tilapia macrocephala* (Bleeker).[1,2]

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(Plates I-III; Text-figures 1-10).

INTRODUCTION.

Teleosts of the family Cichlidae are noted for their elaborate patterns of courtship, mating and parental care, and for the readiness with which they breed in the restricted confines of the small aquarium. It is largely because of these attributes that cichlids have become the subjects of several extensive investigations of fish behavior. Outstanding among these studies are those of Breder (1934) on the blue acara, *Aequidens latifrons*; Noble and Curtis (1939), Peters (1941) and Seitz (1942) on the jewel fish, *Hemichromis bimaculatus*; Peters (1937) on the small Egyptian mouthbreeder, *Haplochromis multicolor;* and Seitz (1940) on a closely related mouthbreeder, *Astatotilapia strigigena.*

These students have investigated topics such as schooling, sex recognition, courtship, territory, social dominance, spawning, parental care, the stimuli causing the release of various innate responses and many other related items of behavior. In these studies, mating behavior has been described qualitatively and in varying degrees of detail. Although the reports in most cases have been based on a number of observed spawnings, the results are given in a generalized or "averaged" form and the only suggestion of variability in behavior is found in such broad phrases as "this *usually* happens," or "the *typical* mode of behavior is." Moreover, the "averaging" is often achieved by means of subjective impressions rather than in terms of a calibrated or objectively weighted evaluation of behavioral characteristics.

Variability is a fundamental characteristic of biological phenomena, a characteristic which always merits careful consideration in studies of animal behavior. It is the writer's belief that the study of teleost behavior cannot extend very far beyond the present descriptive stages unless and until methods of a more quantitative nature are employed. Students of mammalian psychology, and particularly of rodent behavior, have made excellent progress by utilizing quantitative procedures. The present study afforded an opportunity for testing the applicability of comparable techniques in the study of the reproductive behavior of fish.

The present report is concerned with the average behavior and the range of variability under constant aquarium conditions of a type which can be readily duplicated. In other investigations now in progress, mating activities of brain-operated and hormone-treated animals will be compared to the norms obtained in the present report.

Nothing appears to be known concerning the mating behavior of *Tilapia macrocephala* in the wild state, and the present report is hardly intended as a substitute for such an investigation. Nevertheless, wherever the behavior of fishes has been studied both under field conditions and in captivity, agreement has been fairly good, as for example in the Centrarchidae. It is anticipated that the over-all picture obtained in this study should prove to be essentially similar to conditions prevailing in the natural state, and that differences if any would be expected only in some of the lesser details.

LITERATURE.

Information concerning the breeding habits of *Tilapia macrocephala* and of related species belonging to the same genus has been furnished for the most part by aquarium hobbyists and through cursory observations by field naturalists. It is realized that because aquarists' reports often fall below generally recognized standards of scientific accuracy, as might be expected considerable confusion exists in the literature concerning certain aspects of the breeding patterns of *Tilapia.* Some of these difficulties may no doubt be attributed to an improper identification of

the species in question, since aquarists sometimes trust the knowledge and dependability of fish dealers for the identity of their subjects. Nevertheless it is possible to obtain from this literature a rough picture of the reproductive habits of the genus *Tilapia.* For these reasons the inclusion of numerous aquarists' accounts is considered expedient. What may be offered herein is by no means intended to be a comprehensive review of the extensive popular literature.

Brief descriptions of the breeding habits of *Tilapia macrocephala* can be found in the aquarium texts of Stoye (1935), Arnold and Ahl (1936) and Innes (1944). In addition, reports on the spawning of *Tilapia heudeloti* (which according to Boulenger (1915) may be a variety of *Tilapia macrocephala*) have been presented by Breder (1934) and Schoenfeld (1934). These accounts tell us briefly that (1) a nest is built by the mating pair; (2) the female deposits the eggs in the nest; (3) the male fertilizes the eggs as soon as they are deposited; (4) shortly thereafter the male takes the eggs into his mouth; and (5) the eggs hatch and develop in the mouth of the male. How long the eggs are retained in the male's buccal pouch is not indicated, but Stoye (1935) reports two cases where eggs were carried 24 to 29 days respectively. Stoye considers these periods abnormally long as a result of excessive disturbances.

With four probable exceptions, all the species of *Tilapia* whose spawning habits have been reported are mouthbreeders. The four exceptional species remove their larvae to sand pits in typical cichlid fashion. These non-mouthbreeding species are (1) *Tilapia guinasana* (Roloff, 1938, 1939), (2) *Tilapia spaarmanii* (Hey, 1945, 1947; Anon., 1948)[3], (3) *Tilapia melanopleura* (Svenssor, 1933; Bertram, Borley and Trewavas, 1942) and (4) *Tilapia zillii* (Bade, 1923; Stoye, 1935; Arnold and Ahl, 1936; Bertram, Borley and Trewavas, 1942). However, Liebman (1933) describes *Tilapia zillii* as a mouthbreeder. Incubation of the eggs is accomplished by the females of *Tilapia flavomarginata* (Pellagrin, 1906)[4], *Tilapia galilaea* (Pellegrin, 1903, 1905), *Tilapia martini* (Boulenger, 1906), *Tilapia microcephala*[5] (Junghans, 1918) and *Tilapia mossambica*[6] (Bade, 1923; Dietz, 1926; Roloff, 1937; Peters, 1937a, 1939; Seleuthner, 1941; Hey, 1947). The same appears to be true for *Tilapia squamipinnis, Tilapia lidole,* and *Tilapia shirana* (Bertram, Borley and Trewavas, 1942).

The male is credited with the care of the eggs in *Tilapia dolloi* (Asch, 1939), *Tilapia heudeloti* (Breder, 1934; Schoenfeld, 1934),

Tilapia macrocephala (Stoye, 1935; Innes 1944), *Tilapia microcephala* (Schreitmüller, 1920) and *Tilapia simonis*[7] (Lortet, 1875; 1883). However, there is some disagreement on this point since both the male and female are believed to incubate the eggs in *Tilapia simonis* (Pellegrin, 1903; Liebman, 1933), *Tilapia galilaea* (Liebman, 1933), *Tilapia microcephala* (Locke, 1932), *Tilapia nilotica* (Boulenger, 1901) and *Tilapia zillii* (Liebman, 1933). Bodenheimer (1927) claims that females alone incubate the eggs of *Tilapia simonis,* and Arnold and Ahl (1936) claim the same for *Tilapia dolloi.*

Irvine (1947) states that the male or possibly both sexes of *Tilapia discolor* and *Tilapia heudeloti* incubate the eggs, but contrary to the findings of Boulenger, Irvine relegates this function to the female in *Tilapia nilotica.* Liebman (1933) believes that it is quite general in Palestine cichlids for both parents to incubate the eggs, but the number of females performing this function is higher than the number of males so doing.

The length of the incubatory period has been reported for only a few species. Arnold and Ahl (1936) say about 14 days for *Tilapia dolloi;* Schreitmüller (1920) gives 4 to 6 days for *Tilapia microcephala;* Roloff (1937) reports 21 days for *Tilapia mossambica;* Bade (1923) offers a value of 15 days while Dietz (1926) and Seleuthner (1941) both give 13 days as the incubatory period of this species.

The retrieving into the female's mouth of newly released young has been reported for *Tilapia dolloi* (Arnold and Ahl, 1936), *Tilapia macrocephala* (Stoye, 1935), and *Tilapia mossambica* (Roloff, 1937; Seleuthner, 1941) while in *Tilapia microcephala* the male is credited with that activity (Schreitmüller, 1920).

Nest making by these mouthbreeders has received some general attention. On a number of occasions, Lortet (1883) witnessed the female *Tilapia simonis* lay approximately 200 eggs in a small excavation which she had hollowed out and cleaned in the silt among the reeds. Nest building by both the male and the female *Tilapia nilotica* was observed in the field by C. L. Boulenger (1908). Roloff (1937) describes the nest of *Tilapia mossambica* as being 20 cm. in diameter. Seleuthner (1941) reports a nest for this species which was 25 cm. in diameter and reached a depth of 4 cm. in the middle, while Hey (1947) pictures it as a "small saucer-shaped depression." Bertram, Borley and Trewavas (1942) describe the nest of *Tilapia squamipinnis* as a circular depression.

Other mouthbreeding cichlids are listed by Peters (1937) as belonging to the genera *Astatotilapia, Ectodus, Geophogus, Hap-*

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[3] Also recorded in "Report No. 1 (1944) Inland Fisheries Dept., Union of South Africa"—1945.

[4] Designated by Boulenger (1911) as *Tilapia andersonii.*

[5] *Tilapia microcephala = Tilapia heudeloti.* According to Boulenger (1915, p. 178) *Tilapia macrocephala,* and *Tilapia multifasciata* "may ultimately have to be regarded as varieties of *T. heudeloti.* I am unable to find characters by which to separate them sharply."

[6] *Tilapia mossambica = Tilapia natalensis.*

[7] Placed in the genus *Tilapia* by Boulenger (1899) but now referred to a new genus *Tristramella* by Trewavas (1942). Lortet (1875) called this fish *Chromis paterfamilias.*

lochromis, *Pelmatochromis* and *Tropheus*.[8] It is to be noted that at least some of these genera also contain non-mouthbreeding species, suggesting a multiple origin of this habit even within the cichlid family. This problem has been considered in some detail by Breder (1933) and Myers (1939).

The small Egyptian mouthbreeding cichlid, *Haplochromis multicolor*, and a closely related form, *Astatotilapia strigigena*, have been the most popular and intensively studied of all the mouthbreeding fish. In addition to the scientific investigations previously mentioned, more than 30 accounts of the spawnings of these two fish have appeared in the last three decades, the majority of them in the Wochenschrift für Aquarien-und Terrarienkunde. These accounts, which are relatively consistent in their general implications, demonstrate that the spawning behavior of these species differs considerably from that of the various species of *Tilapia* described above. For this reason what is known about the *Haplochromis* and *Astatotilapia* mating patterns is summarized briefly for the purposes of comparison.

In these species the male does practically all of the nest building. Upon the completion of the nest, the female starts the oviposition by depositing between four and ten eggs in the nest. The male immediately fertilizes the eggs after which they are picked up by the female. This cycle is then repeated as the female lays a second batch of eggs. Between five and ten such cycles have been reported by various authors as comprising a spawning. The eggs are carried for 9 to 20 days, after which the young are released. However, the young are taken back into the female's mouth at night and at other times when disturbed. Such a retrieving of the young has been the subject of a special investigation by Peters (1937).

MATERIAL AND METHODS.

Tilapia macrocephala (Bleeker) is native to West Africa, particularly in the region of the Gold Coast. Boulenger (1915) describes the species as coming from the Gold Coast, Ashantee and Lagos. Many of his specimens were taken from the Ancobra river and Secconda lagoon in the Gold Coast, and from the Lagos lagoon. According to Arnold and Ahl (1936) the fish is found in the brackish lagoons of the coast and the swampy deltas of rivers.

The individuals utilized in this study were selected from a laboratory-bred stock which had been maintained for a number of years prior to the start of the present research.[9] Males were chosen for the brightness of their yellow operculum which is a secondary sex

character (Pl. I, Fig. 1). The females (Pl. I, Fig. 2) were selected on the basis of the complementary sex character, namely a deep red spot in the center of the gill cover.[10] These dimorphic color patterns appear at sexual maturity and disappear after castration (Aronson, in manuscript).

Pairs were established by random selection and were placed in 54-liter aquaria, 60 cm. × 30 cm. × 30 cm. each containing roughly 36 liters of water. The side and rear walls of these tanks were painted pale blue to minimize any possible disturbing influences from neighboring tanks, and also to facilitate the ability of the investigator to follow the activities of the fish. The tanks were located in a greenhouse the temperature of which was maintained throughout the year at 26° C. with a positive and negative variation of approximately 3° C. To furnish hide-outs for the fish which at the same time would not obstruct the observer's view, a mat of floating plants was placed in every tank. *Cabomba* was extensively used for this purpose, but *Sagittaria subulata* was found to be somewhat more suitable and was used whenever available.[11] The fish were fed mostly a dehydrated preparation consisting of dried shrimp, oatmeal, beef liver, lettuce and spinach. At times this was supplemented by live tubifex worms. Occasionally the fish nibbled at the stonewort *Nitella*, and this was placed in the tanks when available. The tanks were aerated continuously, and the water was changed whenever it became excessively murky. This was approximately once a month. Tap water brought to the proper temperature was used in washing the tanks and for replacement.

In order to avoid injury to the fish due to excessive nipping which often occurred after spawning, a transparent glass partition was placed in the aquarium, separating the male from the female as soon as observations of oviposition were completed. As the individual carrying the eggs (generally the male) eats little or nothing during the incubatory period, brooding fish were not fed during this interval. By the time that the young were released from the male's mouth, the females often were prepared to spawn again. However preliminary observations indicated that when such spawnings occurred males sometimes behaved abnormally, due apparently to the protracted period of inanition. To avoid this difficulty an arbitrary rule was established to the effect that males were separated by a transparent glass partition from females for one week after they had released their young or had swallowed their eggs. This interval allowed the males to feed and regain their strength. While thus iso-

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[8] An older listing of mouthbreeding cichlids given by Pellegrin (1903) includes the genera *Geophagus*, *Acara*, *Chaetobranchus*, *Tilapia*, *Paratilapia*, *Pelmatochromis*, *Ectodus* and *Tropheus*.

[9] I am greatly indebted to Miss Ethelwyn Trewavas of the British Museum for kindly checking and verifying the taxonomic identity of the fish as *Tilapia macrocephala*.

[10] Examination of this spot by Aronson and Holz-Tucker (in manuscript) has revealed that it is in actuality a semi-transparent window through which the underlying red gill can be seen.

[11] The author wishes to express his appreciation to Dr. Myron Gordon of the New York Zoological Society for furnishing all of the sagittaria used.

lated, females often spawned alone but observations showed that a considerable amount of courtship took place through the glass partition.

To prevent the parents from eating their young after they were released, large masses of the stonewort *Nitella* were placed in all tanks where young were being incubated. The stonewort was distributed equally on both sides of the partition since the newly released fry could easily swim through the cracks at the intersection of the partition and the glass walls of the tank. Disturbances caused the young to swim into the fine interstices of the *Nitella* where they would not be followed by their cannibalistic parents.[12]

The criteria employed to indicate the approach of oviposition were (1) persistent nest building, mostly by the female, (2) heightened courtship activity, and (3) protruding genital tubes. When these signs were observed, continuous records were taken of the courtship and mating activities of the pair up to the time of spawning and for one-half hour thereafter. Attempts were made to secure continuous pre-spawning records for three hours. However, this goal was attained in only a small number of cases with the result that the records vary from just a few minutes before spawning up to the full three-hour span. A serious difficulty was encountered here in that the activities of many promising pairs were observed continuously for many hours up to a whole day without the fish ever ovipositing.

After the present experiment had been terminated, behavior during the interspawning interval was studied, using different pairs of *Tilapia*. The experimental conditions were the same as before with the following minor exceptions: (1) no plants were used but instead inside aquarium filters served as hide-outs; (2) the water in the tanks was never changed; (3) the males

were never separated from the females. The actual spawnings of these pairs were not witnessed, all ovipositions being recorded as having occurred at the time the eggs were discovered in the male's mouth. All pairs were checked twice daily for eggs. A 15-minute record of the behavior of a given pair was taken 5 or 6 days after the spawning and again on the 15th or 16th day. The interval between successive spawnings varies from 8 days up to almost a year with a mode of 15 days (Aronson, 1945). Approximately two-thirds of the intervals are less than 29 days. Thus the 5- or 6-day score serves as an intermediate record for the shorter inter-spawning intervals, while the 15- or 16-day score serves in the same capacity for the longer intervals. Obviously some of the 15-day records could not be taken because of intervening ovipositions. Many of these observations served, moreover, as behavior records for varying days before spawning.

QUALITATIVE DESCRIPTION OF REPRODUCTIVE BEHAVIOR.

In order to furnish the reader with the proper background for the quantitative investigation, it is appropriate to present first a general description of mating activities. This account does not take into consideration the question of the range of variability and any exceptional items of behavior. Details concerning many of the generalizations made here will be considered in the next section.

Certain of the behavioral patterns which increase in their frequency of occurrence prior to spawning and which lead up to the acts of oviposition and fertilization generally are classified as courtship activity. Such behavior appears to express the level of sexual excitability of the given individual. In accordance with the views of Huxley (1914, 1938), Howard (1929) and Marshall (1936), it is assumed that courtship tends to hold the pair together, and through mutual stimulation may lead to a well synchronized spawning. In the terms of Schneirla's (1946) discussion, such relationship may be thought of as involving trophallactic processes, and the temporal aspects of these interactivities are of significance from the standpoint of adaptive function. *Tilapia* eggs (Pl. I, Fig. 2; Pl. II, Figs. 3, 4), as well as those of other oviparous teleosts, are shed in a flaccid state, but rapidly become hard and turgid upon entering the water. That is, they "water harden" (Breder, 1943). Hence, to insure fertilization the male must deposit his sperm over the eggs within a very short time after they are laid. An adequate synchronization of the pair's reproductive processes thus appears to be critically important for effective species survival.

There follows a description of the early courtship behavior of *Tilapia macrocephala*: (1) The male and female approach each other and suddenly dip their heads; or one member of the pair lowers its head. This

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12 This was the author's first experience with the maintenance of tropical fish. Since then, several innovations have been developed. Inside aquarium charcoal filters are now placed in every tank. These keep the water clean and eliminate the need for changing it. Plants are not used since they grow poorly in *Tilapia* aquaria. The food formulae have been modified as follows: (1) *Wet mash*: 2½ lbs. liver; ½ lb. chopped lettuce and spinach; ½ lb. dried ground shrimp (mostly shell); ½ lb. dried and ground refined shrimp (mostly muscle); Pablum (or other pre-cooked infant cereal)—enough to make thick paste (approximately 3½ lbs.); 1 pinch salt. The liver is chopped, about 1 cup of water added, and the mixture is then liquefied in a blending machine. All ingredients are mixed together with sufficient Pablum to make a paste. The food is further solidified and preserved by packing into jars and immersing them in boiling water for about 10 minutes. (2) *Dry food*: 12 lbs. dried shrimp (mostly shell); 12 lbs. dried refined shrimp (mostly muscle); 10 lbs. liver; 6 lbs. chopped lettuce; 6 lbs. chopped spinach; 28 lbs. Pablum; 2 level teaspoons salt. The ground spinach and lettuce are mixed with the Pablum and cooked for 15 minutes. The liver is cut into slices and boiled for 15 minutes in a minimum amount of water and then chopped. All ingredients are mixed together and the resulting paste spread about ½ inch thick on trays. When almost completely dry, the food mixture is ground and sifted through screens of several coarsenesses.

The sexes are no longer separated after the spawning. If the fry are to be saved they are forcibly removed from the parents' mouths on the tenth day post-oviposition, and are placed in small aquaria. At this age the young do very well without further parental care, and thus, losses through cannibalism are easily avoided.

behavior has been termed "head-nodding." (2) When one member of the pair approaches the other, spreads its opercula and expands its buccal pouch, we have called this act a "throat-puff." (3) The male or female ceases swimming movements and the trunk musculature appears to quiver for a fraction of a second. We have named this a "body-quiver." (4) When one member of the pair slaps the other with its tail, this has been called a "tail-slap." Included in this category were the frequent cases where tail-slapping motions were quite distinct, but where actual contact with the partner was not made.

Closely associated with the courtship acts, but displayed as well in many pairs throughout the interspawning interval, is a mode of behavior which we have termed "nipping." This occurs when a fish swims after its partner, and then with a sudden dart nips or bites the body of its mate. Nipping also occurred at times without a previous chase. Sometimes the male and female may nip each other simultaneously and occasionally they may even lock jaws. Frequently observed cases in which the pursuing fish darts ahead but misses the fleeing opponent also have been included under the general heading of nipping.

In addition to its association with courtship and spawning, nipping behavior appears to be related to the establishment of social hierarchies and the formation of territories. These further relations of nipping have not as yet been investigated.

The above-mentioned patterns of behavior usually appear as quite distinct, but occasionally they tend to merge into one another, so that discretion on the part of the observer is often called for in assigning a particular courtship act to its proper category. Oftentimes two or more courtship acts may be displayed in rapid succession, a frequent combination being a head-nod, throat-puff and body-quiver. Another commonly occurring combination is the throat-puff and tail-slap.

Readers acquainted with the courtship behavior of other cichlid fishes will readily recognize the resemblance of the *Tilapia* pattern with those of other cichlids. Reactions such as the body-quiver, the throat-puff and the tail-slap in some form seem to be prevalent throughout the family.

Nest-building is first observed after intensive courtship has been in progress for several hours or days. Most of this activity is conducted by the female who begins scooping up mouthfuls of gravel from scattered locations in the bottom of the tank. Soon the excavating is confined to one location, and the construction of a nest begins. Often two or more nests are constructed prior to the spawning, and sometimes nests are built and then destroyed during the construction of an adjoining nest. The nests are most often round or slightly oval. If the gravel substratum of the aquarium is not too thick, the fish dig down to the slate bottom of the

tank. If, however, the depth of the gravel is more than 2 or 3 cm., the nests do not reach the slate.

In our study the length of time taken to complete a nest varied considerably from as little as one-half hour up to what appeared to be several days. In the latter case, the nest-building activity occurred in spurts, followed by periods of quiescence. The rapid builders generally worked continuously until the nest was completed. A small amount of nest-building was accomplished by sweeping movements of the tail and pectoral fins. However, this has been interpreted as incidental to swimming and balancing movements and not directly related to nest building.

After the nest is more or less completed, nest-building decreases considerably and is supplanted to some extent by nest-cleaning (Pl. I, Fig. 1) in which the female, and occasionally the male, pick continuously at the bottom of the nest. Nest-building and nest-cleaning are always interspersed among various phases of courtship responses.

As the nest takes form, the genital tubes of the male and female become more prominent. At this time, the male begins to swim slowly over the nest, rubbing his genital tube over the bottom. We have called this "passing-nest." Later when the female completes the nest, she likewise "passes-nest." Thus the pair circle around and around, rubbing their genital tubes over the nest. This behavior is often interrupted by periods of courtship, nest-building and nest-cleaning activity. As soon as a fish starts passing-nest, the genital tubes become fully erected, but if this activity ceases for a time, the tubes generally recede somewhat. This suggests that mechanical stimulation is one factor causing the erection of the genital tube. Since fish not on the verge of spawning are sometimes seen with partially extended genital tubes, other stimuli seem to be involved in the partial erection of the genital tubes. Courtship activity and hormones are suggested as possible factors.

After the passing-nest behavior of the male and female has been in progress for some time, the female stops in the nest during a "pass-nest," and her body musculature quivers for a second or two. This has been called a "spawning-quiver." Males also exhibit spawning-quivers, but in the male these responses generally are less distinct and are seen less frequently.

Spawning-quivers were the final pre-spawning acts and indicated the imminence of the oviposition. During one of these quivers a batch of approximately 10 to 20 eggs is extruded by the female in what we have termed an "oviposition movement" (Pl. I, Fig. 2). The female then swims just past the nest. She is followed by the male who passes-nest, usually rubbing his genital tube over the newly laid eggs and sometimes exhibiting a spawning-quiver. This complementary act has been termed a "fertilization movement" (Pl. II, Fig. 3). Sperm

apparently are emitted at this time, although no male products were apparent in our observations. The female then repeats her oviposition movement which is followed closely by a second fertilization movement of the male. After two to four such egg-laying cycles, the female swims rapidly from the nest for a distance of 15 to 30 cm., then faces the nest. Meanwhile the male swims in the vicinity of the nest for a minute or so, then rapidly picks up the eggs with his mouth (Pl. II, Fig. 4; Pl. III, Fig. 5).

In our investigations there were a few exceptional cases where the male did not pick up the eggs. Then the female nipped and tail-slapped the male violently, exhibited some courtship behavior, and finally after 10 to 20 minutes of this activity she picked up the eggs and carried them in her mouth (Pl. III, Fig. 6). We found that at times, because of the unequal sizes of the male and female, all the eggs could not fit into the male's mouth, the female would pick up the remaining eggs, but not until 10 to 20 minutes had elapsed.

Post-spawning activity consists for the most part in poking around the nest, first by the male, and later by the female as well. If any of the eggs are missed when the original spawn was picked up, they are almost always recovered during this poking activity.

After several minutes, this poking behavior sometimes gives way to extensive nipping and mouthing in which one member of the pair, generally the female, soon dominates and the other retreats into hiding.

The eggs hatch in 5 days and are carried from 2 to 15 days further, during which time the embryos continue to develop. The young are released abruptly and most of them are sufficiently developed at this time to suggest that further parental care would not be advantageous to them. Parental care appears to end suddenly with the release of the young. In fact, parents sometimes eat their newly liberated offspring. Never did we see the young swim back into the parental mouth as has been described by some authors for this and other *Tilapia* species, and which is such a striking characteristic of the small Egyptian mouthbreeders, *Haplochromis multicolor* (Peters, 1937).

With this brief description of the mating pattern we turn now to an analysis of the actual counts made of the frequency of occurrence in relation to the time of spawning of many of the behavioral acts described above.

Analysis of the Mating Pattern.

For the purpose of analyzing the data, records were organized in the following manner. For each observed spawning, the time of appearance of the first batch of eggs was designated as the zero minute. The 15-minute period just prior to the zero minute was called the first pre-spawning interval. The period 15 minutes to 30 minutes prior to the zero minute was named the second pre-spawning interval. Twelve pre-spawning

intervals were similarly measured. Again starting from the zero minute, the 15-minute interval which followed was called the first post-spawning interval, and a second post-spawning interval was likewise measured. The number of times that the various courtship and mating activities (tail-slaps, passing-nest, etc.) were recorded during each 15-minute pre- and post-spawning interval was determined for both the males and the females for all observed spawnings. With data assembled in this manner, a series of distributions was obtained (one of each behavior pattern of both the male and female for each interval). Almost all of these were strongly skewed to the right. The arithmetical mean obviously is a poor representation of the central tendency of a markedly skewed distribution. Medians are generally more suitable, but a better method of treating such data is to employ a transformation. In many cases by use of the transformation $X = \sqrt{x}$, binomial distributions were obtained which could be treated as normal curves.[13] These were checked by plotting cumulative distributions on arithmetic probability paper. However some of the distributions were not normalized following the above transformation, but approximated closely the Poisson series. This was particularly true with infrequently occurring items, where the highest frequency was zero and where the mean was considerably smaller than one. Theoretical Poisson distributions were calculated from Pearson's (1914) tables and the goodness of fit of the actual distributions was tested by the chi-square method.

Still other distributions did not approximate either the normal or Poisson series. As will be noted later, these were not subjected to further statistical analysis.

For the normal distributions, the means, range, theoretical range ($M \pm 3\sigma$), standard deviation and standard error of the mean were calculated. These were plotted graphically in a time sequence, using the method of comparing ranges and means developed by Dice and Leraas (1936) as modified by Simpson and Roe (1939). Since the length of the pre- and post-spawning records varied inadvertently for each spawning, the calculated means for each interval are based upon a varying number of spawnings. Simpson and Roe (1939) point out that the method of Dice and Leraas is less reliable when the frequencies and standard errors of the mean vary greatly. Therefore, in critical cases where the graphic method was suspected of being inaccurate, P values were calculated. The solid lines in Text-figs. 1-6, 8 and 9, indicate females; the broken lines males. The heavy vertical lines designate actual ranges of the distributions. The adjacent light vertical lines indicate theoretical ranges ($M \pm 3\sigma$). The large dots represent the means, while the short horizontal lines above and

below the means indicate the range of M ± 2σ$_M$. When these ranges overlap, it may generally be assumed that the differences between the means are not significant. Conversely, if M ± 2σ$_M$ do not overlap, the differences between the means are significant. The limitation of this method has already been noted.

For the Poisson series, the theoretical ranges were considered to run from zero to that value of the variate having a relative frequency of .003 or less. Means were compared by the method described by Snedecor (1946). Because of the asymmetrical nature of the Poisson distribution the graphical method of comparing means described above cannot be used. Hence, in the following graphs, the range of M ± 2σ$_M$ are not indicated for the Poisson distributions.

Where the distributions did not conform reasonably well to either a normal or Poisson series, only the means and actual ranges are presented on the graphs.

The 15-minute records on the 5th or 6th post-spawning day and on the 15th or 16th day were treated in a similar manner. Since a number of pairs spawned again within two weeks after these observations were made, it was possible to use some of these data as records of behavior on the 2nd, 5th, 6th, 9th and 12th pre-spawning days. Because of the small number of cases, only means and ranges are indicated graphically.

THROAT-PUFFS. As seen from the graph in Text-fig. 1, the females (solid lines) exhibited this behavior very rarely on the several days they were observed before spawning. One female throat-puffed just once on the 9th pre-spawning day. However, by

three hours before spawning, the throat-puffing frequency had reached a rather high level, which was maintained with little fluctuation right up to the spawning. Immediately after the egg laying, throat-puffing activity increased sharply. To be sure that this rise was not due to chance fluctuation, the means of the first pre- and post-spawning intervals were compared and were found to differ significantly (P < .01).

The males showed the throat-puffing behavior much less frequently than the females (Text-fig. 1, broken lines). On the several days the pairs were observed prior to the spawning, no throat-puffing by the males was seen. At three hours before the egg laying, a low frequency of throat-puffing was recorded, and this level was maintained up to the spawning. When these data were treated by utilizing the transformation X = √$\overline{x}$ as already described, the frequencies of male throat-puffs were found to be distributed in a Poisson fashion with zero the highest frequency, an indication that the mean frequencies were less than one. This raised the question whether the males of just a few pairs were responsible for the bulk of the throat-puffing activity. A partial answer to this question was obtained by selecting the 25 spawnings in which continuous records for the first hour before spawning were available. It was found that during this hour, 64.0% of the males exhibited no throat-puffing at all. This contrasts with the figure of only 4.0% for the female. Similarly, in the seven pairs where continuous records for the first two pre-spawning hours were available, 57.1% of the males did not throat-puff. From this we may conclude that a consider-
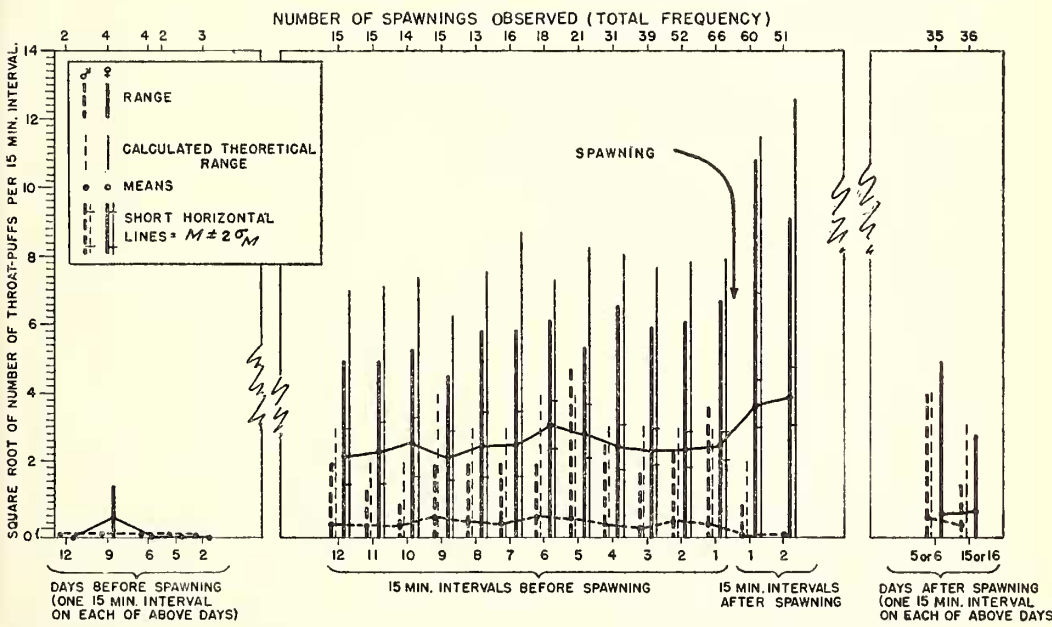
TEXT-FIG. 1. Fluctuation in male and female throat-puffing behavior before and after spawning.
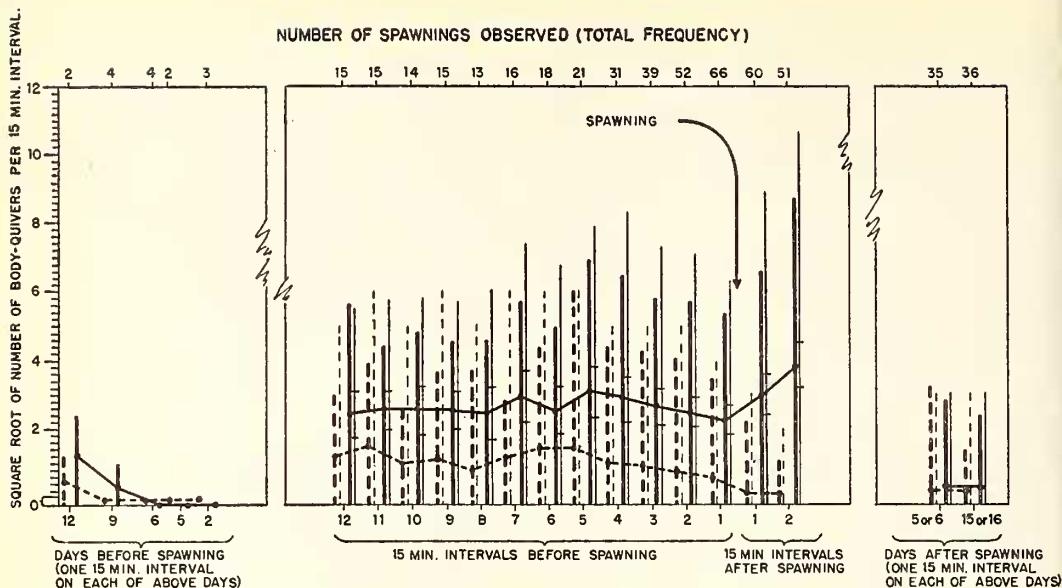
TEXT-FIG. 2. Fluctuation in male and female body-quivering behavior before and after spawning.

able number of males exhibited little or no throat-puffing behavior prior to the spawning.

Immediately after the egg laying, throat-puffing by the male was no longer observed. Since the mouths of the males were now filled to capacity with eggs, it seems better to say that after the spawning throat-puffing could not readily be identified. By the 5th or 6th post-spawning day, many of the males were no longer carrying eggs, and now the throat-puffing behavior had reached the pre-spawning level.

BODY-QUIVERS. Only an occasional body-quiver was exhibited by the males and females on the several days they were observed

prior to the spawning (Text-fig. 2), but by three hours before oviposition the body-quivers (solid lines) were very frequent occurrences in the female. They remained at this relatively constant level until the spawning, after which there was an abrupt rise. The means of female body-quivers for the first pre- and post-spawning intervals were compared, and the latter were found to be significantly higher ($P = .021$). At five days after spawning the females' body-quivering had dropped far below the immediate pre-spawning level, and remained the same during the observation period on the 15th or 16th day.

The body-quiver frequency of the males at
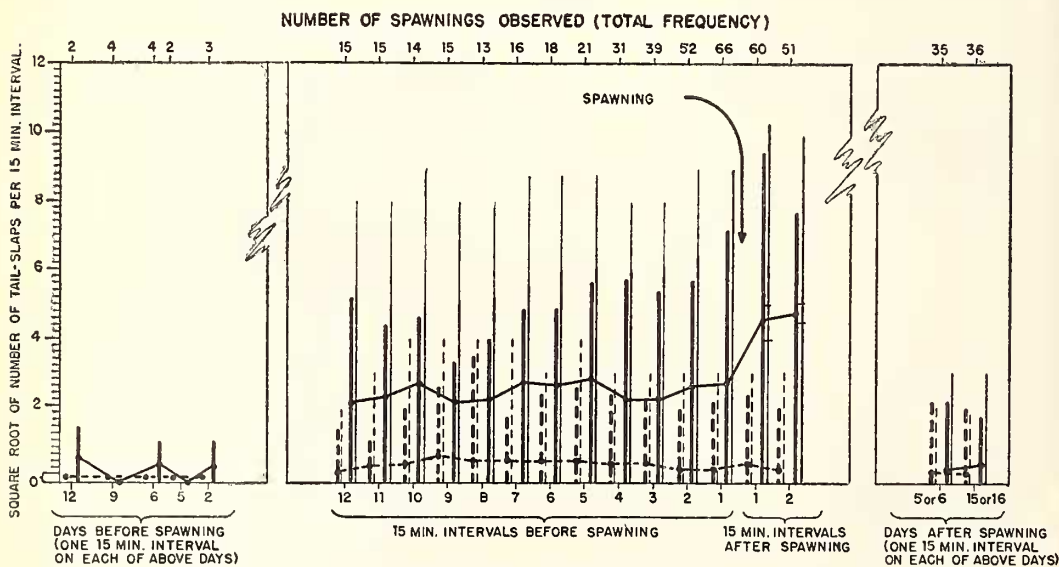
TEXT-FIG. 3. Fluctuation in male and female tail-slapping behavior before and after spawning.
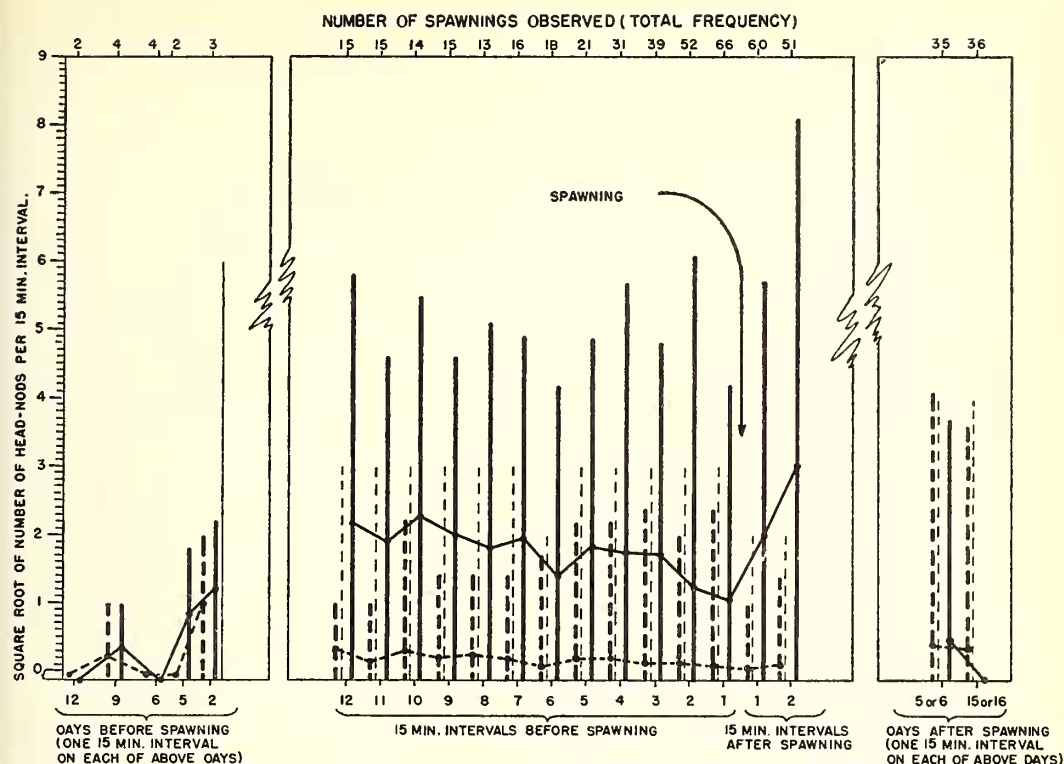
Text-fig. 4. Fluctuation in male and female head-nodding behavior before and after spawning.

three hours before spawning was considerably less than the females' and again these data were best treated as Poisson distributions. The behavior remained at this level until the fifth pre-spawning interval when it started to slope off, reaching a minimum at the first pre-spawning interval. However, when the male body-quivers of the fifth and first pre-spawning intervals were compared, this slope appears not to be significant $(P > .10)$. On the 5th or 6th post-spawning day, and on the 15th or 16th post-spawning day, the body-quiver frequency of the males was very close to that of the females.

Of the 25 spawnings in which continuous records were available for one hour before the spawning, 100% of the females and 80.0% of the males exhibited body-quivering at least once. In the seven ovipositions in which continuous two-hour pre-spawning records were taken, 100% of the males gave body-quivers at least once. Thus while this courtship pattern is exhibited more frequently by the females, practically all males show some body-quivering activity prior to the egg laying.

TAIL-SLAPS. With the transformation previously described, the data of both the male and female were found to be distributed in a Poisson fashion, excepting the first two post-spawning intervals of the female which were normally distributed (Text-fig. 3). On the several days prior to the spawning occasional tail-slapping by the female was observed, but at three hours before the egg laying, the occurrence of this behavior had increased considerably. This level was maintained until the spawning, when there was another significant rise $(P < .01)$ during the first post-spawning period.

No tail-slapping by the male was observed on the several days prior to the spawning, and during the three-hour pre-spawning interval, the frequency of tail-slaps remained low with relatively little fluctuation. Approximately this same frequency was observed during all the post-spawning observation periods.

Of the 25 pairs for which continuous records for the first hour were obtained, 100% of the females were recorded as tail-slapping at least once, but only 48% of the males. In the seven spawnings with two-hour continuous pre-spawning records, 71.4% of the males tail-slapped at least once.

HEAD-NODS. Following the transformation, head-nodding data for the female was characterized by a large number of zero frequencies and a small number of rather high frequencies. These did not fit Poisson distributions. At times, head-nodding was not clear cut and easy to recognize, and it is possible that a considerable amount of head-nodding passed unrecognized. Before the spawning, head-nodding activity was quite high (Text-fig. 4), at least for some of the
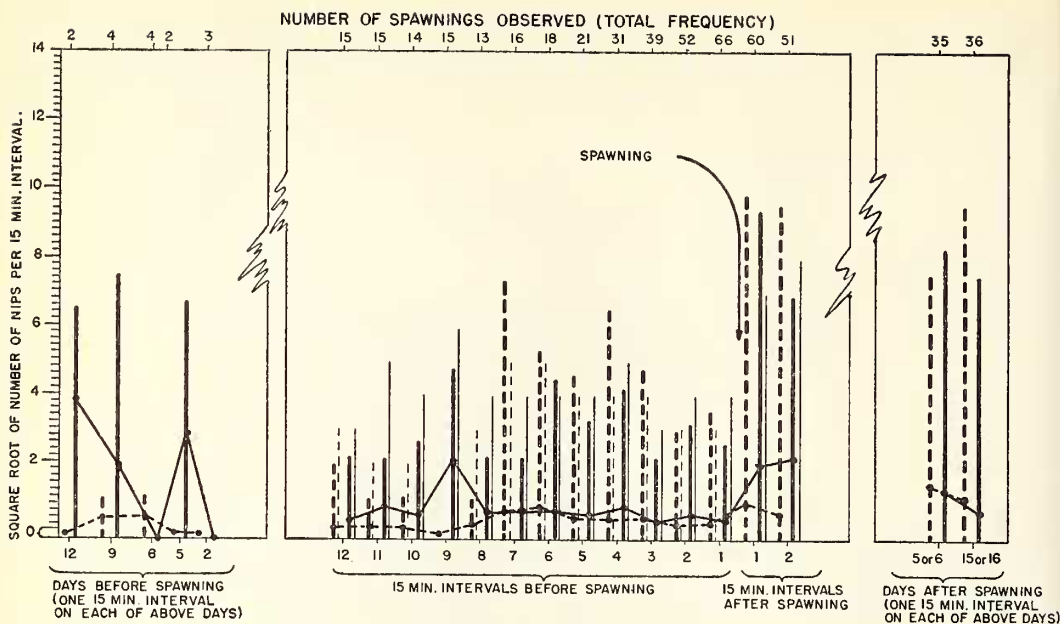
TEXT-FIG.5. Fluctuation in male and female nipping behavior before and after spawning.

females, and there was a still further rise after the egg laying.

The data for male behavior fit Poisson distributions quite closely. The low mean values indicate that this behavior occurred rather infrequently, and little fluctuation was noticeable before or after the spawning.

Of the 25 ovipositions from which continuous records were taken for the first prespawning hour, 84.0% of the females and only 20.0% of the males exhibited head-nodding at least once. Similarly, of the seven pairs where two-hour records were available, 100% of the females and 28.6% of the males head-nodded at least once. We may conclude that head-nodding is a typical female activity and that a small fraction of the males head-nod occasionally.

NIPS. Nipping data of both the male and female were treated as Poisson distributions. Both sexes displayed some nipping behavior on the several days they were observed before the spawning (Text-fig. 5). During the three-hour pre-spawning observation period, approximately the same amount of nipping was shown by both the males and females. After the egg laying there was a significant rise (P<.01) in the nipping frequency of the females. The rise in female nipping during the ninth pre-spawning interval may be significant (P = .05), but it was mostly due to a marked spurt of activity of a single female.

Analysis of the 25 spawnings where complete records for the first hour before spawning were taken showed that 68.0% of the females and only 28.0% of the males exhibited nipping behavior at least once. Where two-hour continuous records were available, 100% of the females, and 57.1% of the males

engaged in some nipping activity. This suggests that practically all of the females and at least half of the males do some nipping before spawning.

NEST-BUILDING ACTS. On the several days before spawning, nest-building by either the male or female was not observed (Text-fig. 6), but by the third hour before oviposition, female nest-building activity had reached a rather high frequency. Since the presence of a nest and the occurrence of nest-building behavior was one of the more important criteria used to determine the imminence of spawning, and hence to ascertain the appropriateness of starting the observation, these data are likely to be somewhat biased in favor of early nest-builders. Actually at three hours before spawning, the average nest-building activity of the female may not be as high as that indicated by the data.

The drop indicated in the seventh prespawning interval appears not to be significant if the nest-building values of the fifth and seventh intervals are compared (P = .13). On the other hand, there is a noticeable downward slope between the fifth and first pre-spawning intervals, and when these two intervals are compared, the difference was found to be highly significant (P<.01). It is clear that female nest-building behavior drops off as the time for the laying of the eggs approaches, and it is gradually superseded first by nest-cleaning behavior (which is clearly distinguishable from nest-building), and secondly by nest-passing activity, which, as we shall see in the next section, is increasing as the nest-building frequency is declining.

Following the oviposition episode, nest-building activity dropped to a very low fig-
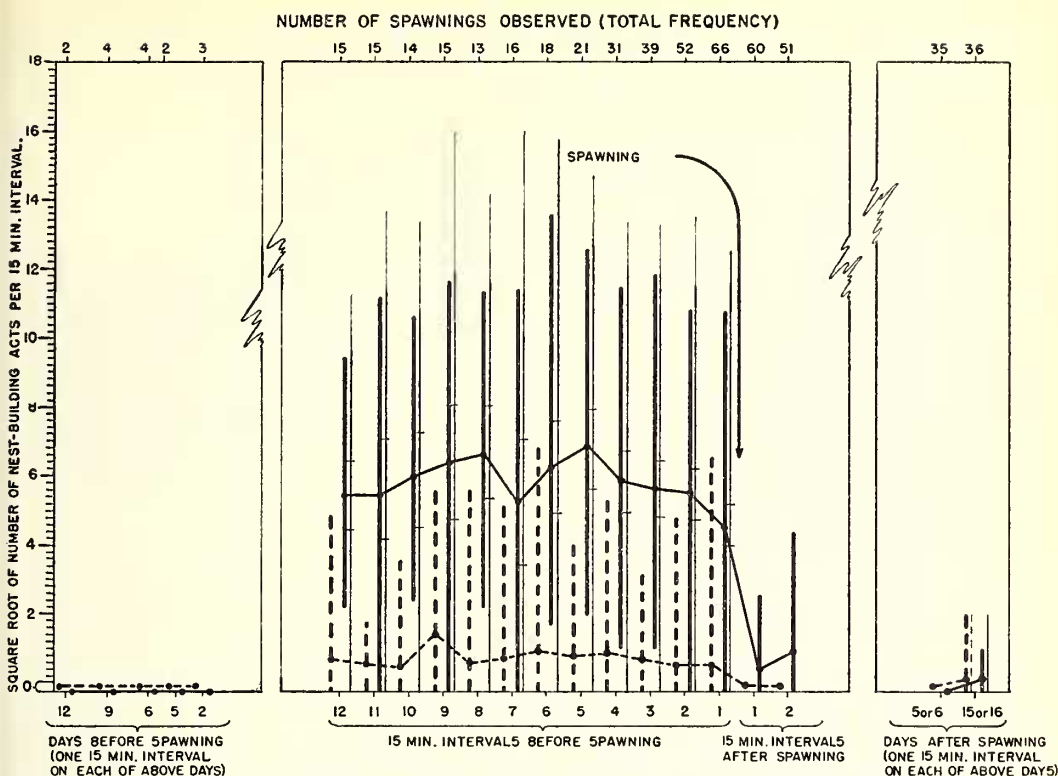
TEXT-FIG. 6. Fluctuation in male and female nest-building behavior before and after spawning.

ure. On the 5th or 6th day nest-building by females was not observed, and on the 15th or 16th day only one nest-building act was observed during the 15-minute observation interval by one female out of thirty-six.

The data for the male was characterized by high frequencies of zero values and low frequencies of high values which nevertheless did not fit Poisson curves even after the aforementioned transformation. In contrast to the extensive nest-building activity of the female, that of the male was quite limited. Similar to the female, there is a downward slope in activity between the fourth and first pre-spawning intervals. However, the decline is not very pronounced and its statistical validity could not be readily ascertained. After the spawning the males no longer engaged in nest-building except for a single male which on the 15th post-spawning day nest-built four times during the observation interval. This male was paired with the one female, which was also observed to build a nest during the 15-day post-spawning interval. Two nests were present in the tank and it is apparent that this pair was approaching another spawning cycle.

Turning again to the 25 spawnings with continuous records for the first pre-spawning hour, it was found that 100% of the females and 72% of the males engaged in nest-building at least once. Of the seven pairs with continuous two-hour pre-spawning records, 71.4% of the males did some nest-building.

It is probable that only a small percentage of males do not engage in any nest-building prior to the spawning.

Fifteen nests built by ten pairs were measured shortly after the spawnings. In each case the fish were first carefully removed without damaging the nests. Since in many cases the nests were oval, two diameters were taken, namely the short diameter, and at right angles to this the long diameter. The points used in these measurements are indicated in Text-fig. 7. The average short diameter was 11.8 cm., the average long diameter 13.2 cm., and the average depth 2.6 cm. The female fish (which as shown above are primarily responsible for the construction of the nests) varied from 10.7 gr. to 19.2 gr. with an average of 15.1 gr. The males were slightly heavier, weighing on the average 18.0 gr. There was no indication from these limited data of a correlation between size of fish and size of nest.

PASSING-NEST. The earliest nest-passing by the female was recorded for the eleventh pre-spawning interval, two and one-half hours before the egg laying (Text-fig. 8). Following the previously mentioned transformation, the data for this interval fit a Poisson distribution. The same is true for the records of the 6th, 8th, 9th and 10th intervals. The data for the 2nd to 5th and the 7th intervals consisted of a series of zero or very low frequencies and a smaller group of relatively high values, vaguely suggesting
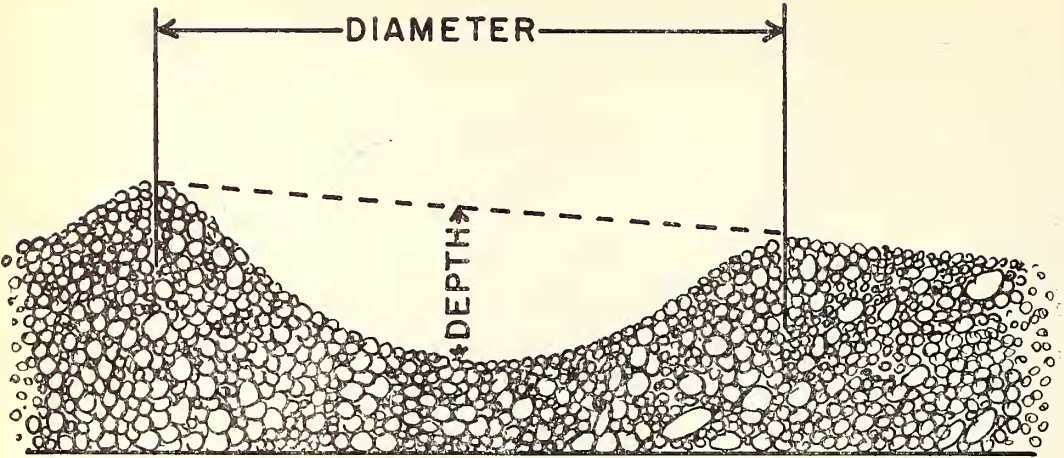
TEXT-FIG. 7. Diagrammatic section through typical *Tilapia* nest showing points used for nest measurements.

bimodal curves. The data for nest-passing for the first interval were normally distributed. These data indicate a gradually rising frequency of nest-passing as the spawning approached, with a sudden spurt of activity during the second and first intervals. After the egg laying, nest-passing activity of the female dropped to almost zero and none was recorded on the 5th or 6th and 15th or 16th days.

The nest-passing data of the male were normally distributed for the first interval. The records for the remaining pre-spawning intervals were highly skewed to the right with highest frequencies zero, which, however, did not fit Poisson series. While no

nest-passing was recorded for the males on the several days prior to the spawning, a substantial amount of nest-passing was observed by three hours before the egg laying. This level of activity remained fairly constant until the second interval when it started to rise precipitously. However, during the first pre-spawning interval, the nest-passing activity of the female surpassed that of the male for the first time ($P<.01$). After the spawning, the frequency dropped to almost zero and nest-passing was not observed on the two post-spawning observation days.

Observations indicated that male and female nest-passing were not entirely independent of each other, and calculation of the
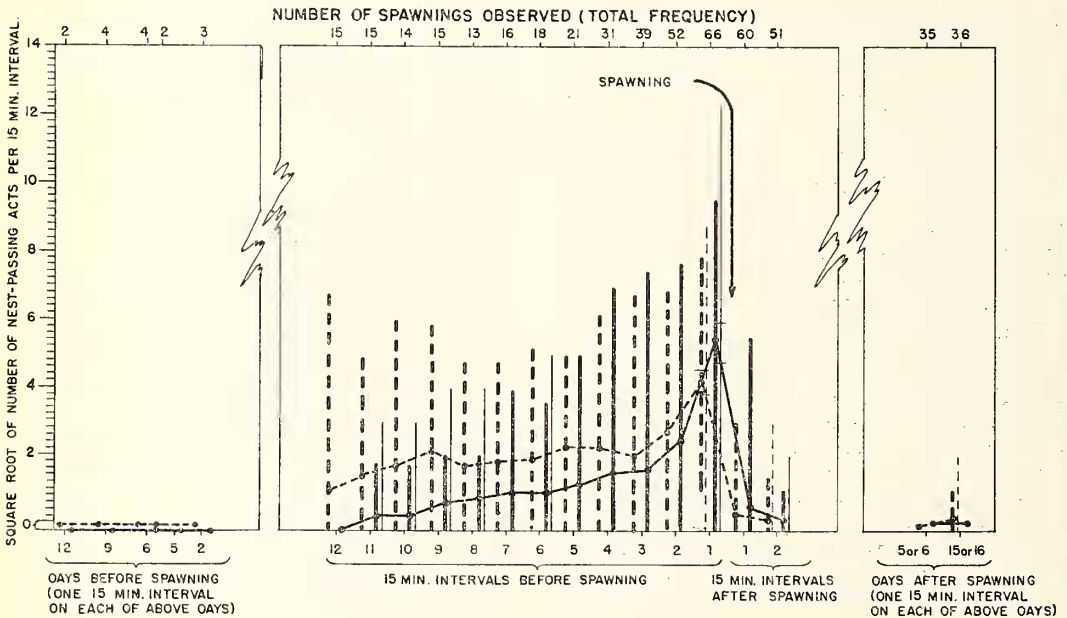
TEXT-FIG. 8. Fluctuation in male and female nest-passing behavior before and after spawning.
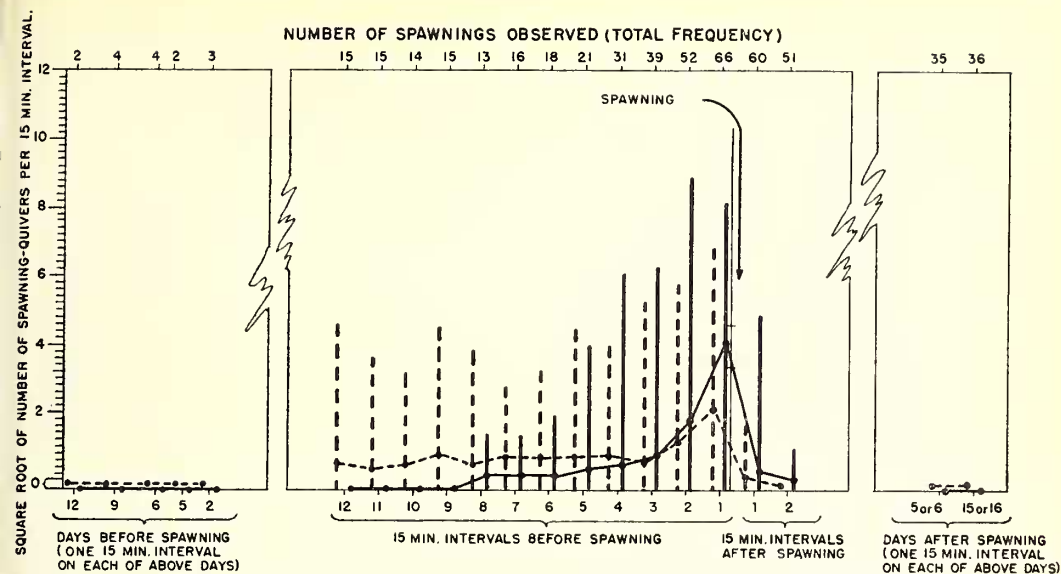
TEXT-FIG. 9. Fluctuation in male and female spawning-quiver behavior before and after spawning.

coefficient of correlation for the first pre-spawning interval yielded an r of $+ .63$. This was transformed to $Z = + .74$ which is a highly significant correlation ($P < .01$). The nest-passing data for the remaining pre-spawning intervals appear to be comparably correlated, but the data do not readily lend themselves to this type of statistical treatment. Prior to the spawning, all of the males and females exhibited some nest-passing activity.

SPAWNING-QUIVERS. This behavior was not observed during the observation periods on the several days before the spawning (Text-fig. 9). Female spawning-quivers were first seen during the 8th pre-spawning interval, 1¾ to 2 hours before the egg laying. Their frequency gradually increased and reached a peak during the first pre-spawning interval. There was a marked drop to almost zero after the egg laying, and on the 5th or 6th days and 15th or 16th days none were seen.

A few male spawning-quivers were in evidence during the 12th pre-spawning interval, and a low level of this behavior was maintained until the second interval, 20 to 15 minutes before the egg laying, when there occurred an abrupt rise in frequency which terminated during the first interval. During the first post-spawning interval, a very few spawning-quivers were recorded, and none were seen thereafter. While a few of the males exhibited spawning-quivers long before the females, the peak of spawning-quiver activity of the females during the first pre-spawning interval was considerably higher than that of the males. However, the data did not permit further statistical analysis.

Selecting the 25 spawnings for which continuous records for the first hour before oviposition were available, it was observed

that 96.0% of the females and 72.0% of the males showed at least one spawning-quiver during this hour. Similarly, in the seven spawnings for which two-hour continuous records were available, 100% of the females and 71.4% of the males were recorded as performing at least one spawning-quiver during these two hours. It thus appears that while all the females showed this behavior, in about a fourth of the males spawning-quivers could not readily be distinguished from nest-passing behavior. Since all of the females exhibited spawning-quivers and because of the sharp peak in the frequency of occurrence of this activity just before the spawning, this behavior can also be employed as an indicator of the approaching oviposition.

OVIPOSITION AND FERTILIZATION. The behavioral patterns considered thus far were recorded in terms of the number of times that the acts occurred during a short interval of time (i.e., 15 minutes), and the relative infrequency of some of this behavior accounts in part for the marked skewness of the distribution curves. On the other hand, the oviposition data which follow, and the data concerning the reactions of the male and female to the eggs and young, are based upon the total frequency of the behavior during a given spawning, and as might be anticipated, these data approximated more closely binomial distributions which could be treated as normal curves.

A nest-passing act by the female during which eggs were oviposited was counted as a single oviposition movement. A nest-passing act by the male when eggs were present in the nest was recorded as a fertilization movement. Actual contact with the eggs was not considered essential as a criterion for a fertilization movement, although in most

instances the male rubbed his genital tube over some of the freshly laid eggs.

In 76 observed spawnings, the mean number of oviposition movements by the female was 3.41 ± .13 with a standard deviation of 1.1 movements. The mean number of male fertilization movements was 3.46 ± .15 with a standard deviation of 1.3. The difference between the means is .05 ± .2 which indicates clearly that the number of oviposition movements of the female does not differ significantly from the number of fertilization movements of the male. Finally, there is a significant positive correlation $(r = + .48,$

$z = + .52,$ P calculated from $\frac{z}{\sigma_z} < .01)$ between these two activities, indicating that the number of times the males fertilize the eggs is partly related to, and probably dependent upon the number of oviposition acts of the female.

PARENTAL BEHAVIOR. In a total of 76 observed spawnings, the male alone picked up the eggs in 62 cases (81.8%), the female picked up the eggs in 6 cases (7.9%) while both male and female participated in this activity in 8 cases (10.5%).

The time after the beginning of oviposition for the male to start picking up eggs varied from 20″ to 2′10″ with a mean of 1′3″ ± 3″ and a standard deviation of 23″. For the female this interval varied from 3′18″ to 11′14″ with a mean of 7′59″ ± 1′22″ and a standard deviation of 3′17″. The difference between the means of these two distributions is obviously significant, and from these data we may conclude that the male starts to pick up the eggs as soon as the oviposition has terminated, while the female allows several minutes to elapse before she will collect any of the eggs still available. Here then is an apportioning mechanism which results in the observed fact that the male usually incubates the eggs, and the female does so on infrequent occasions.

Eggs remain in the nest available to the female under two circumstances. First, if the male's mouth is of insufficient size to contain all of the eggs, a few may be left over in the nest. This was the situation in case 1 (Table I) where a small male was paired with a large female. It was quite clear to the observer that in this instance not all of the eggs could fit into the male's mouth. Secondly, eggs would be available to the female when the male behaved atypically and did not touch the eggs. In three of these cases males had released broods seven to twelve days previous to the spawnings, and this may be a contributing factor causing the lack of response of the males to the eggs.[14] In most instances where the eggs remained in the nest for any length of time, the females would chase, nip and court the males. In a few cases, the latter retaliated and violent

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14 On the other hand, recent observations by Aronson and Holz-Tucker (unpublished) reveal that males in the process of incubating young may on occasion fertilize and pick up a new batch of eggs.

TABLE I.

Time from the Beginning of Oviposition for Eggs to Be Picked Up. Eight Cases Where Both Male and Female Engaged in This Activity.

Case No.	Male		Female	
	Start	Finish	Start	Finish
1	25″—	50″	7′15″—	
2	11′00″—	11′30″	6′50″—	10′10″
3	3′00″—	4′00″	2′30″—	4′00″
4	4′05″—	4′30″	4′15″—	4′30″
5	2′05″—	5′00″	4′30″—	5′00″
6	4′10″—	5′10″	4′10″—	4′55″
7	6′24″—	10′30″	5′50″—	6′36″
8	3′50″—	4′00″	1′25″—	3′30″

fighting ensued; as a result the nests were destroyed and the eggs scattered. In cases 3, 6, and 7 (Table I), as soon as the female began to pick up the eggs, the males followed suit and both gathered up the eggs simultaneously. The typical pattern when eggs are left in the nest may be summarized as follows:

(1) Immediately after the eggs are oviposited and inseminated, there is often a period of extreme quiescence lasting a minute or two.

(2) This is followed by a period in which the female appears to be inhibited from approaching or touching the eggs, but at the same time she seems to be excited by the eggs, resulting in active nipping, chasing and courting of the male who sometimes responds similarly.

(3) After several minutes the inhibitory action of the eggs begins to diminish; the female now approaches the nest, pokes around the eggs, and eventually picks them up. It was at this time that several of the recalcitrant males listed in Table I also approached the nest and in a few cases started to pick up eggs ahead of the female.

It is suggested that in cases 2 to 8 (Table I), chasing, nipping and courting by the female, and also her poking around the nest, sufficiently stimulated the male to pick up the eggs, thereby completing the pattern.

Once started, the length of time it took for males to gather up the spawn varied from 2″ to 1′45″ with a mean of 13″ ± 2″ and a standard deviation of 16″. The high variability noted here is a result of two exceptional cases, one where the male took 1′7″ and in the other 1′45″. In the remaining 60 spawnings, the time was less than 46″. On the other hand, six females took from 35″ to 3′ with a mean of 2′6″ ± 22″ and a standard deviation of 51.7″. Thus we see that not only does the female wait longer before starting to pick up the eggs, but once started she performs this task at a significantly

slower rate. In most cases, the males gathered up the eggs rapidly and then kept poking around the nest for some time. Thus any scattered eggs were quickly recovered. Some of the females, on the other hand, would pick up part of the eggs, swim away from the nest, return and pick up more eggs, swim away again, and so forth.

The egg-gathering records for the female were necessarily limited by the behavior of the males as noted above. It was therefore considered appropriate to use for comparison data from other experiments. Aronson and Holz-Tucker (unpublished data) observed the spawning of an isolated female that could see another female in an adjacent tank. The ovipositing female took 24' to start gathering up the eggs and the process itself took 1'25" to complete. Similarly, we observed the spawning of a completely isolated female. This female did not start to pick up the eggs for 13'5". She took 1'15" to gather up most of the spawn, but left six eggs which she did not pick up for another eight minutes. A large number of normal females were paired with males suffering various types of brain lesions (Aronson, in manuscript). In 27 spawnings, these females took on the average 12'2" to start picking up eggs and an average of 1'15" to complete the job. Hence these data support our original conclusions. However, it is likely that in our first observations, the mean time for the six females to start picking up the eggs is somewhat low, while the time it took to complete the process may be a little too high. It is of interest to note that in a few spawnings the females seemed unable to carry all of the eggs that they themselves had laid.

Both the male and female are capable of successfully incubating the eggs. The percentage of spawnings in which young were recovered at the termination of the incubatory period is shown in Table II. Where the spawnings were not witnessed, the slightly higher score made by the males may be accounted for by a possible failure to record

a few cases where the spawn was swallowed immediately after the oviposition, and before it was observed. The data for the third set of observations are taken from a second experiment, (Aronson, 1945). These spawnings were also not witnessed. In this experiment, aquarium conditions were considerably improved by the use of aquarium filters, thus avoiding any changes of water. The young were forcibly ejected from the parental mouth on or about the tenth day after spawning and were counted immediately, thus largely eliminating the possibility of losses through cannibalism.

Even with these improved techniques, only 40% of the males released viable fry. Two factors account for this low yield of young by the males. First is the failure of the eggs to be properly fertilized, or death of the embryos, with subsequent disintegration of the eggs. A second factor is swallowing the spawn. The relative importance of these two factors will now be considered.

If freshly laid unfertilized eggs are placed in a jar of *Tilapia*-conditioned water which is kept at approximately 26° C., very few of the eggs will show any gross signs of degeneration before 24 hours. Starting with the second day, however, some of the eggs will have decomposed, and in all cases few if any intact eggs remain after the tenth day. As to the variation in the length of the incubation period, it will be seen in columns 6 and 7 of Table III that females may carry unfertilized eggs for as long as ten days, after which time it may be assumed that all have decomposed. Note particularly that in almost 80%[15] of these cases, the dead eggs were retained longer than one day, and it is highly probable that in many of these cases the eggs were carried until they were quite degenerate. It was not unusual to examine the contents of a male's or female's mouth and

[15] Since the presence of incubating eggs was checked only twice daily, spawn swallowed shortly after oviposition might have been overlooked. Hence this figure may be a little too high.

TABLE II.

Per Cent. of Spawnings in which Young Were Recovered.

	No. of spawnings in which males incubated eggs.	No. of males releasing young.	% of males releasing young.	No. of spawnings in which female incubated eggs.	No. of females releasing young.	% of females releasing young.
Spawnings witnessed.	68	22	32.4	14	3	21.4
Spawnings not witnessed.	85	33	38.8	2	0	0.0
Spawnings not witnessed, 2nd experiment.	70	28	40.0	4	4	100.0

TABLE III.

Variation in Length of Incubatory Period.

Length of incubation.	NO YOUNG RECOVERED						YOUNG RECOVERED			
	Incubated by males[1].		Incubated by females[1].		Incubated by females[2] (unfertilized eggs).		Incubated by males[3].		Incubated by females[1,4].	
	No. of males.	Per cent. of males.	No. of females.	Per cent. of females	No. of females	Per cent. of females	No. of males.	Per cent. of males.	No. of females.	Per cent. of females.
0- 1 hr.	1	2.2	5	45.5	54	20.1				
1- 8 hr.	1	2.2	1	9.1						
8-24 hr.	6	13.3	0	0.0						
2 days.	7	15.6	1	9.1	54	20.1				
3 "	13	28.9	1	9.1	34	12.7				
4 "	10	22.2	2	18.2	44	16.4				
5 "	1	2.2	0	0.0	31	11.6				
6 "	2	4.4	1	9.1	19	7.1				
7 "	1	2.2			19	7.1	1	1.2		
8 "	0	0.0			6	2.2	1	1.2		
9 "	0	0.0			5	1.9	1	1.2		
10 "	2	4.4			2	.7	2	2.5		
11 "	1	2.2					12	14.1		
12 "							8	9.4		
13 "							18	21.2		
14 "							12	14.1		
15 "							9	10.6		
16 "							4	4.7	1	33.3
17 "							11	12.9	1	33.3
18 "							2	2.5		
19 "							1	1.2	1	33.3
20 "							3	3.5		

[1] All spawnings witnessed.

[2] Females isolated from males. Spawnings not witnessed. Incubation intervals less than 1 day were recorded as one day, but some short intervals might have been missed. Data from Aronson (1945).

[3] Some spawnings not witnessed. Includes data from Aronson (1945).

[4] The young from the four females of the 2nd experiment indicated in Table II were forcibly removed from the parents' mouths on the 12th day. Hence these cases could not be included in this table.

find that the fish had been carrying a mass of badly decomposed eggs, or a mixture of decaying eggs and viable embryos. From the appearance of the eggs it was frequently apparent that the fish had been carrying the dead eggs for many days. In columns 2 and 3 are listed the durations of the incubatory intervals for males carrying fertilized eggs. It will be noted that in 17.7% of the cases, the spawn was swallowed within 24 hours. The indirect evidence cited above leads to to the conclusion that these eggs were swallowed because of some failure of the male's incubatory mechanism, whereby the male failed to discriminate between eggs and food. On the other hand, those egg masses which were retained in the mouth for a number of days were only swallowed when they had become extensively decomposed. It should be noted in passing that decomposed eggs are never found in the tanks, and it is assumed that they are swallowed rather than spat out. The stomach contents of several males were examined shortly after the egg layings, while the males were carrying eggs. In two of these cases a few eggs were also found in the stomachs.

Columns 4 and 5 show that in 54.6% of the spawnings in which eggs are picked up by the females, they were swallowed within 24 hours and in most cases within the first hour after spawning. Although these data are limited, they indicate that the female's incubatory mechanism is not as dependable as the male's, and that the female fails to distinguish eggs from food much more frequently than does the male.

The length of incubation by the male in cases where young are recovered is shown in columns 8 and 9 of Table III. These data fit closely a normal curve, and from them we have determined a mean incubatory time of $13.8 \pm .27$ days with a standard deviation of ± 2.6 days. This would give us a theoretical range of 6 days to 22 days. The few cases in which the female successfully reared young fall well within this range.

Thus far, only the presence or absence of eggs and developing embryos have been considered. Now, the relative sizes of the spawn and brood will be examined. A new group of pairs was established, and on the day of or day after oviposition, the spawn was ejected from the male's mouth and was counted. This count may be taken to represent fairly accurately the number of eggs laid by the female, since, in most instances, all of the eggs are picked up and few if any are swallowed. Eighty females whose mean weight was $7.15 \pm .38$ gr. deposited an average of 49.7 ± 1.96 eggs.

In a second group of 31 pairs in which the average weight of the females was only slightly less $(5.6 \pm .38$ gr.), the males were allowed to incubate the eggs and the fry were counted soon after their release. Here it was found that the average brood size was only 23.9 ± 2.9 young. It was thought at first that this smaller brood size might be attributed

to the lesser weights of our second group. To examine this hypothesis the body weights of the females that had just oviposited were compared with number of eggs in the spawn. A low order positive correlation was found, which was probably significant ($r = +.23$ or $z = +.236$; P calculated from $\frac{z}{\sigma_z} = .05$). A similar comparison of the weights of females (determined immediately after oviposition) with the size of the brood that was eventually recovered after being incubated by the male partner did not yield a significant correlation ($r = +.10$ or $Z = +.10$; P calculated from $\frac{z}{\sigma_z} = .6$). When two regression lines are plotted (calculated by the method of least squares), one for the rise in number of eggs oviposited as body weight increases, and a second for the change in number of young recovered as body weight increases (Text-fig. 10), the relationship involved becomes clearer. From these regression lines in Text-fig. 10, it can readily be seen that for females of the same body weight, the number of young successfully incubated is considerably smaller than the number of eggs laid. This loss can best be accounted for by the failure of some of the eggs to be fertilized and by the death of some of the embryos. Since brooding fish have never been observed to spit out decomposed eggs or embryos, and since such material has rarely been observed on the gravel substrata of the aquaria, it is assumed that the incubating fish somehow manages to sort out and swallow this dead matter.

These data also indicate that while larger females tend to lay a greater quantity of eggs than smaller females, the number of fry successfully brooded by the males remains constant regardless of the weights of the females and hence of the magnitude of the spawn. Therefore the mortality of eggs and embryos must be directly proportional to the size of the female and hence to the number of eggs laid. Since the larger females were in most cases older, this difference might be based upon an aging factor. It is also conceivable that such increased mortality was due to overcrowding in the male's mouth during incubation.

It is an interesting fact that incubating *Tilapia* generally carry some gravel intermingled with eggs. Of 63 fish examined on the day or day after the egg laying, 95.2% were carrying one or more pieces of gravel. Generally between 25 and 50 pieces (commercial grade No. 2) were found along with the eggs, and occasionally the count went well over 100. The possible significance of this fact is not known at present. It is not clear whether or not the gravel is picked up accidently along with the eggs, and whether this behavior bears some relation to the survival of the embryos. For example, it is possible that since the eggs and gravel are continuously churned around in the mouth, the
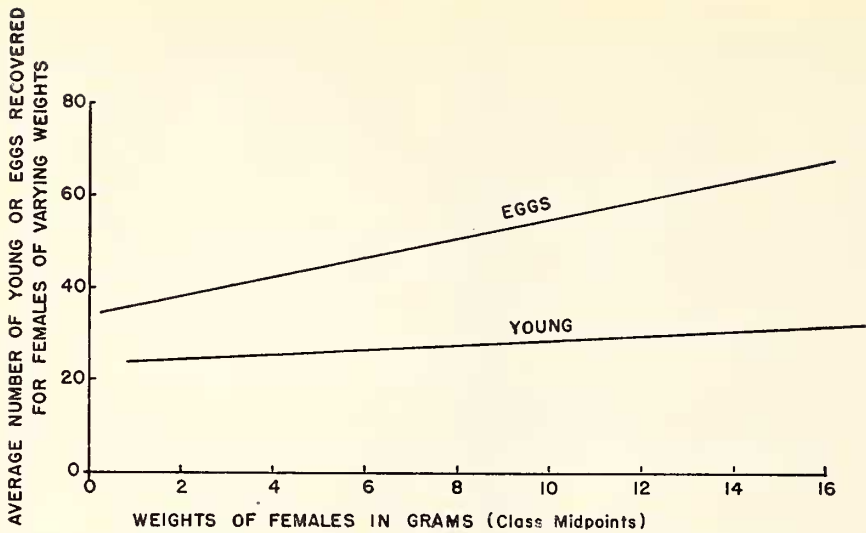
TEXT-FIG. 10 Regression lines showing relation of body weights of females to number of eggs laid during each spawning and relation of body weights of females that spawned, to number of young recovered immediately after their release by the incubating males.

latter might serve to rub off fungi or ecto-parasites from the developing fish.

It is important to note that there is considerable variability in the number of days that given parents may incubate their young. It is therefore to be expected that at the time of release, the broods carried longest will be the ones furthest advanced in development. This, generally speaking, is found to be true. Thus, fry released in less than ten days still have a large yolk sac and their swimming activity is sporadic, whereas young incubated for longer intervals show little or no trace of the yolk sac, also their swimming ability is developed to the stage where they are well able to elude their enemies if reasonable shelter is provided. A complicating factor is that, as can be seen from the few samples in Table IV, there is a considerable difference in the rate at which the fry grow within the parental mouths. Thus the average size of a given brood incubated for 22 days was barely larger than another one incubated only 15 days. Similarly, a given brood retained in the mouth for only 11 days reached the same average size as another brood incubated for 16 days. It is possible the number of young in the brood may somehow be related to growth rate; however, our limited data on this point in Table IV do not suggest such a relationship. It is also of interest to note that the variation within the brood was quite low, the average coefficient of variation (V) for nine broods being 3.7. This state of affairs is in striking contrast to the great variability (V = 15 ± 1.60) which resulted when a brood was kept together in a stock tank from the time of release to maturity (Aronson and Holz-Tucker, in manuscript).

DISCUSSION.

In most vertebrates the characteristic mating behavior patterns of the two sexes are distinctly different. Thus in the rat, the reproductive habits of which have been analyzed most intensively, the typical pattern of the estrous female, lordosis, is only occasionally exhibited by the male (Beach, 1938, 1945). Similarly, the typical male pattern of ear-wriggling, mounting and pelvic thrusts is seldom seen in the female (Long and Evans, 1922; Hemmingsen, 1933; Beach, 1938).

The sex difference in behavior generally is very clear although relative rather than absolute. Under special conditions males may be induced to exhibit female-like behavior, and the reverse can also be accomplished (Beach, 1941). The conditions producing such results often are very special in nature. Thus for example, the well known fact that estrous cows frequently exhibit male-like mounting behavior may very well result from the almost universal custom of segregating the cows from the bulls. Similarly Beach and Rasquin (1942) explain in part the high incidence of masculine behavior in their female rats as the result of repeatedly testing two females together. These authors are also aware of the possibility that the females of their particular colony may have been more active in a masculine direction than are females from most other stocks. However, we are concerned with the fact that disparity of behavior between sexes is general among the vertebrates.

A survey of the literature indicates that in reptiles a behavioral dichotomy of the sexes appears to be the rule, and the writer's extensive investigations of the sexual be-

TABLE IV.

Relation Between Average Size[1] of Young in Brood and the Number of Days the Brood Was Incubated.

No. of days young were carried.	No. of fry in brood.	Average length of fry[1] (mm.).	Coefficient of variation.
10	13	9.2 ± .08	2.9 ± .57[2]
11	19	10.6 ± .10	4.0 ± .65
11	3	10.4	....
11	8	9.8 ± .09	2.8 ± .70
12	44	10.8 ± .06	3.9 ± .41
14	18	9.4 ± .11	5.1 ± .85
15	82	11.2 ± .04	3.3 ± .26
16	58	10.6 ± .06	4.4 ± .40
16	38	10.6 ± .06	3.7 ± .43
22	58	11.5 ± .05	3.4 ± .31

[1] Length from tip of mouth to end of tail fin.
[2] Standard error of the coefficient of variation.

havior of the tailless amphibia have shown that in the Anura, male and female sexual behavior are quite specific with only occasional evidence of bisexual behavior (Noble and Aronson, 1942; Aronson, 1943, 1943a, 1944).

In many birds these distinctions are less clear. Thus in the pigeon, billing and bowing are common to both sexes (Whitman, 1919), and while it is usual for the female to squat and for the male to mount, copulation not infrequently occurs with the positions reversed (Carpenter, 1933).

While all vertebrates appear to possess the neuromuscular and hormonal mechanisms capable of eliciting most elements of the mating pattern of the opposite sex (Beach, 1942, 1947), morphological differences, particularly in the genitalia, hormones and other genetic factors, greatly limit the incidence, completeness and effectiveness of such behavior. Thus in the majority of vertebrates, behavior patterns characteristic of the male or female are readily distinguished.

In contrast to this typical vertebrate condition, *Tilapia* appears to represent an extreme condition. None of the patterns of reproductive behavior investigated are entirely characteristic of either sex. Qualitatively, male and female courtship and spawning behavior are exactly alike. Even in the acts of oviposition and fertilization, the overt motor patterns are the same in both sexes. Both fish swim slowly over the nest and rub their genital tubes on the substratum. The one observable difference occurs when eggs extrude through the genital aperture of the female, while the male's genital tube releases sperm, which, however, are invisible to the naked eye. It is only when the frequencies of the various reproductive acts are considered that behavioral differences between the sexes become apparent. It is true even so that in *Tilapia* sex differences in behavior depend in some cases on the time interval before the spawning. Thus, as we have found, the females exhibit much more court-

ship and do most of the nest-building. Males do more nest-passing than the females at one to two hours before the spawning, but at 15 minutes prior to oviposition we find this relationship clearly reversed. After the spawning, both qualitative similarity and quantitative dichotomy are still in evidence. Thus males wait on the average only 1.3' before they start to pick up eggs; whereas females require on an average 7'59". Also, males pick up the eggs much faster than the females, and are less prone to swallow their eggs.

In some of the patterns, as for example head-nodding, the quantitative difference between male and female frequency of the act is sufficiently large that such behavior could possibly be called a female pattern. However, our data have shown that in 25 pairs where continuous records for the first hour were available, almost one-third of the males exhibited some head-nodding. It is highly probable that if the entire span of the pre-spawning sex behavior could be observed, an even greater percentage of the males would be found to perform a minimal amount of this behavior. Bisexual or homosexual activity has generally been thought of as a recognizable intrusion of the characteristics of behavior in one sex to a greater or lesser extent into the behavior patterns characteristic of the opposite sex. Such partial observations of sex dichotomy are known to occur in a limited portion of the population or under special circumstances such as segregation. Thus we are justified in considering bisexual or homosexual behavior a rather restricted phenomonon in most vertebrates. It follows that in the case of *Tilapia* none of the patterns should be relegated to one particular sex as is generally done in the higher vertebrates.

One might hypothesize that this situation in *Tilapia* represents a primitive condition in the evolution of reproductive behavior patterns. This, however, is doubtful since cichlids are a highly specialized family of

teleosts, and on the other hand clearly recognizable, sexually divergent mating patterns are in evidence in some of the anatomically more primitive fishes. While our study of the described condition concerns *Tilapia*, it is apparent from the literature that qualitative similarities and quantitative differences such as we find between male and female sexual behavior in this species will be found to a greater or lesser extent in all cichlid fishes, and may well be true of several other families of fish.

Rather than being a primitive condition, we might view these behavior patterns of *Tilapia* as adjustments (in an evolutionary sense) to a specialized mode of reproduction in which the similarity of the sex behavior patterns has a considerable adaptive value. For the post-spawning parental behavior this point is fairly evident. If both sexes are capable of rearing the young, there is less likelihood of lost or wasted spawn. If we look upon the action of courtship as a mutually stimulating and a synchronizing mechanism as well as one which keeps the pair together, one might expect the sexes to develop comparable mechanisms to accomplish the same outcome when not limited by morphological dissimilarities.

Not all behavioral disparities between the sexes in *Tilapia* are readily understandable. On several occasions, males exhibited considerably more courtship activity than the females of given pairs. In no case did such excess lead to a spawning. One observation showed a male in a stock tank courting at a very high frequency as he swam around the enclosure. In the same aquarium a female was engaged in building a nest. Actually she did not court in relation to this sexually active male, but rather her activities had to do with two other males in the territory. The significance of excessive courtship by males is not clear. It is possible that it represents the equivalent of bisexual behavior, that is, of males behaving like females.

In this study we have found it convenient to group certain activities such as the throat-puff, body-quiver, tail-slap and head-nod under the category of courtship, as distinct from subsequent items of the reproductive series, namely nest-building, nest-passing, spawning-quivers, oviposition and fertilization. However, no sharp line of demarcation is implied between these. If we follow the functional definition of courtship as previously stated (page 136), one cannot altogether exclude the latter group of patterns from the courtship category. However, a separation on the basis of functional or adaptive significance seems to be in order. Thus courtship behavior is mainly concerned with the formation and maintenance of the pairs while the latter activities have most to do with the immediate preparation for spawning, as for example the building of the nest and the physiological preparation for oviposition and fertilization. Also there are indications of an organic separation. It is of interest to note in this connection that in our observations on the several days before spawning, most of what we are terming courtship activities were seen at one time or another, but the acts of nest-building, passing-nest and spawning-quivers were never recorded. Thus in general reproductive behavior tends to arise and function in group fashion.

The quantitative records show that all of the courtship responses of the female increased in frequency directly after spawning. The same was true for nipping. Two factors appear to be responsible for this increased activity. The first is a physiological change consequent to oviposition, and the second is the presence of eggs. While we have not attempted to analyze the relative influence of these two factors, several observations are of interest here. First, the observed heightened courtship activity generally lasts several hours and subsides gradually. Secondly, the activity continues long after the eggs have been removed to the male's mouth. The freshly laid eggs might possibly release some type of chemical stimulus, but the evidence for this is not forthcoming. Moreover, if newly oviposited eggs are presented to males and females that have not spawned recently, such eggs are generally eaten within a short time, and they do not stimulate either courtship or nipping. The effect of this heightened activity is not apparent in most of the spawnings, but in the few cases where the males are slow in picking up the eggs, the courting seems to attract the male to the nest and stimulates him to gather up the spawn.

It has long been recognized that certain external morphological characteristics of an animal, together with specific modes of behavior, may act as exciting stimuli to other members of the species (and sometimes to members of another species) for the mediation of specific behavioral responses. Lorenz (1935, 1937) has developed this concept as a cornerstone of his theory of instinctive behavior. The stimulus or group of related stimuli bringing forth a reaction are called "releasers," the responding individual is designated as the "companion." Mutual instinctive responses of companions are sharply separated from learning processes although some modifications of the former are recognized. Furthermore, according to this view the release of every unconditioned reaction is considered to be dependent on a special central nervous mechanism which is called the "innate releasing schema" (Lorenz, 1935) or "innate releasing mechanism" (Tinbergen, 1939, 1948).

These hypotheses have become quite popular on the Continent. In this country they have received some consideration by students of bird behavior, but they are largely out of tune with the findings and interpretations of a large segment of the American experimental psychologists (Lashley, 1938) who in general have paid little attention to the

Lorenz movement. To say that a special "innate releasing mechanism" exists for every unconditioned reaction implies an extreme localization of function within the brain, a claim that is without special support in this country. Here the more popular view is that most responses are capable of being elicited by a broad array of well separated stimuli (Beach, 1942, 1947) and are not exclusively dependent upon any single stimulus or group of stimuli. Moreover, there is here a growing tendency to think of innate and learned factors as closely interlocked in their influence on behavior (Schneirla, 1941, 1946) with the view that in the higher vertebrates at least, purely innate behavior patterns as entities may be simply matters of a convenient terminology doubtfully related to reality. Lack (1940) has criticized Lorenz's view as being too simple. He points out that in many cases the designated releasers may not be the sole characters that bring forth the response. Rand (1941) has been to date Lorenz's severest critic. According to Rand, the releasing characters are by far too limited, and the releasers and responses are mostly unidentified. The reality of releasers has accordingly not been demonstrated but remains presumptive. Actually the experimental analytical approach to behavior is not only untried by Lorenz, but its validity is denied. Finally, according to Rand, there is in Lorenz's treatment a negativistic approach which denies the possibility of ever being able to elucidate the fundamentals of behavior.

Tinbergen (1939) has modified Lorenz's hypotheses in several respects. First, releasers are called "signals" or later "sign stimuli" and are subdivided into releasing stimuli and directing stimuli. More important, Tinbergen recognizes a closer relation than does Lorenz between innate responses released and modifiable factors such as learning, endocrine reactions and neural processes (summation, conditioning and "higher mental processes"). Most important is Tinbergen's recognition of the validity of the experimental approach, and his attempts, mostly by means of artifacts and models, to demonstrate releasers in this manner. Even so, it must be emphasized that Tinbergen sees releasers as very specific and limited morphological and behavioral characters which during the unfolding of a complex pattern of response will hold to a relatively rigid sequence.

Seitz, a follower of Lorenz and Tinbergen, has analyzed the behavior of two related cichlid fishes, namely a small Egyptian mouthbreeder, *Astatotilapia strigigena* (1940) and the jewel fish, *Hemichromis bimaculatus* (1942) in terms of the releaser concept. Seitz recognizes whole series of very specific releasers which call forth specific responses and which lead in an orderly manner to the spawning. These he has summarized in schematic form (1940, p. 82; 1942, p. 100). Thus, in *Astatotilapia*, the presence of a female releases a change to mating coloration in the male, and this change in its turn releases a slight but not significant color change in the female. The presence of the female also releases a mode of behavior called by Seitz an introductory presentation which in turn brings forth a passive response in the female. This in turn releases a complex of movement and color change called by Seitz a "Fegebalz" (lit., sweeping courtship dance). This Fegebalz of the male releases a following reaction on the part of the female, which in its turn releases circular swimming in the male around the spawning site. The circular swimming then releases a strong following reaction of the female to the spawning site which in turn brings forth a response whereby the male slips under the female. This releases circling movements in the female which in turn release the same movements in the male. The circling movements of the male call forth additional circling movements by the female. These release the oviposition movements and the latter release the fertilization movements of the male.

Our experiments were not designed to test the releaser concept and this discussion is not intended as a critique thereof. However, we were interested in learning to what extent our data would or would not support the releaser hypothesis or fit into that pattern of thought.

The significant correlation between male and female nest-passing behavior appeared most likely to fit in with this concept if we were to assume that nest-passing of male and female released a like behavior in the opposite sex. However, we had on record any number of cases where the females were very quiescent, exhibiting little or no courtship or pre-spawning behavior of any kind, and yet the males nest-passed consistently. Of course, the nest itself might be a releaser of nest-passing, but this would contradict a large portion of our data where nest-building by the female and the presence of a well-formed nest was not followed by nest-passing on the part of the male. Similarly in the spawning of the completely isolated female previously referred to, the order of magnitude of nest-passing behavior was well within the range of variability of our control pairs. Yet there was nothing in that situation which could be considered a releaser. In an attempt to follow the lead of Seitz, we could possibly view the various courtship patterns previously described as releasers. For example, the approach-throat-puff of the female might be construed as a releaser of similar behavior by the male which in turn might be thought of as releasing female nest-building behavior. This may be especially so since an approach-throat-puff by a female was often followed by a similar pattern in the male, and soon thereafter the female turned to the construction of the nest. However, no consistent pattern of this type was in evidence. Female throat-puffs were also followed by almost any of the other courtship patterns or by no particular re-

sponses of the male. Again, female nest-building was sometimes preceded by the throat-puffs but often by head-nods, tail-slaps or body-quivers. It is recognized that in general observation, that is in "just watching" these fish, one could easily gain the impression that certain acts are in effect releasers, and others a response to these releasers. However, when observational technique involves an orderly and complete quantification of response according to condition of occurrence, the data do not support such an interpretation.

We are inclined to view the courtship and pre-spawning items of behavior together with the territory and nest as having a general stimulatory effect upon the other member of the pair which would tend to raise the level of sexual excitability in the latter. Or, to put the matter in another way, the given conditions may serve to lower the threshold for the elicitation of various courtship and pre-spawning patterns. Here the particular response obtained would depend upon a whole complex of factors including the neural threshold, the immediate topographic relation to the partner, the territory, the nest and other environmental conditions, as well as the internal physiological balance of the individual at the moment. In this sort of system, no specific releasing stimuli may be properly postulated. For example, a series of weak or only partially effective tail-slaps by the female might bring forth a response in the male similar to one very effective approach-throat-puff. Moreover, as the general level of excitability of both members of the pair increased, there would be a gradual shift in the statistical probability of the elicitation of a given type of response. In other words, throat-puffing during the early stages of the pre-spawning history of a pair might bring forth additional throat-puffing or other phases of the courtship, while later, such behavior might elicit return to the nest or nest-passing. As spawning approached, nest-passing behavior of one member of the pair was often followed by like behavior of the other member of the pair, but this was often interrupted by some of the early phases of courtship such as head-nodding and tail-slapping. In many of the records, interruptions of the smooth flow of passing-nest and spawning-quivers were noted within minutes of the actual oviposition. While these data do not altogether contradict the releaser concept, it is believed that these findings can be more satisfactorily understood by adhering to a considerably more generalized interpretation of the complexity and effectiveness of the stimuli than the "releaser concept" implies.

Seitz (1940) and Tinbergen (1948) in their discussion of releasers refer to the "rule of heterogeneous summation" which states that the release of a given behavior pattern may result from the summation of several different stimuli. Tinbergen also emphasizes that "high internal motivation may cause the reactor to respond to all objects offering the minimum adequate external stimulation." Finally, Tinbergen observes that some releasers have a general excitatory influence, rather than to direct the reactor's response. If these three principles noted here are sufficiently expanded, some of the major objections to the releaser concept are thus overcome, and except for the sharp lines drawn between instinct and learning processes, we begin to arrive at a common ground for the understanding of the nature of sexual behavior.

Summary and Conclusion.

Qualitative descriptions and quantitative measurements of the patterns of reproductive behavior of the African mouthbreeding cichlid fish, *Tilapia macrocephala* (Bleeker), have been presented. These patterns have been grouped into three categories. The first, namely courtship, includes head-nods, approach-throat-puffs, body-quivers and tail-slaps. Most of the females exhibited these courtship items during the observation periods, and at a relatively high frequency. The males performed these courtship acts at a considerably lower frequency. A high percentage of males showed some tail-slaps and body-quivers, and it is believed that if the entire spans of the pre-spawning activity of the pairs could have been observed, all of the males would have performed these courtship patterns. On the other hand, it appears that a measurable portion of males do not head-nod or approach-throat-puff prior to the spawning.

It is hypothesized that courtship behavior is an expression of the level of excitability of the individual. It may be thought of as a trophallactic process which through mutual stimulation serves to regulate the behavioral activities and physiological processes of the male and female so that well synchronized spawnings result.

Nipping, which is closely related to courtship and which also appears to be mutually stimulating, was performed equally by the male and female before the spawning, but nipping on the part of the female rises sharply directly after oviposition. Similar post-spawning increases on the part of the female were noted for all of the courtship patterns. It is suggested that the physiological changes following oviposition plus the presence of eggs are the factors responsible for this heightened activity. During the inter-spawning interval, a low level of courtship is in evidence, especially on the part of the females.

The second group of reproductive patterns includes those acts which are concerned with the immediate preparation for spawning. Included here are nest-building, nest-passing, spawning-quivers, oviposition movements and the act of fertilization. Considerably more nest-building is exhibited by the

female than by the male, but it is likely that all males do some nest-building before every spawning. With passing-nest and spawning-quivers the frequency is somewhat higher for the males an hour or so before spawning, but at 15 minutes before spawning this relationship is clearly reversed, with the females at the height of their nest-passing and spawning-quivers. A significant correlation between male and female nest-passing during the first pre-spawning interval suggests that this behavior is mutually stimulating. The mean number of oviposition movements of the female did not differ significantly from the mean number of fertilization acts of the male. Moreover these behavior patterns are highly correlated, suggesting that the number of times the male fertilizes the eggs is partly related to and probably dependent upon the number of oviposition movements of the female. In contrast with the courtship patterns, behavioral items in the present category were not observed during the inter-spawning interval.

The third category of reproductive acts are those associated with the care of eggs and young. Males start picking up eggs on an average of 1'3" from the beginning of oviposition. Females, if given the opportunity, took on the average 7'59". This is the apportioning mechanism whereby males usually incubate the eggs, and females do so only on infrequent or special occasions. Similar quantitative differences were found in other phases of the parental pattern. Thus females gather up the spawn more slowly and are more prone to swallow the eggs.

A low order positive correlation was found between the size of the female and the number of eggs laid during a given spawning. Since brood size shows no correlation with the size of the female, it is concluded that a greater mortality occurs in the larger broods. Incubating fish generally carry some gravel intermingled with the spawn, but it was not clear whether this bore any relation to the survival of the embryos.

In the majority of vertebrates there are distinct qualitative differences between the patterns of reproductive behavior of the male and female. While both sexes have the neuromuscular mechanism capable of eliciting both the male and female patterns, bisexual or homosexual behavior is limited and generally appears under special conditions. *Tilapia* are exceptional in this respect insofar as there are no distinct qualitative differences between male and female in their sexual activities. However, there are marked quantitative differences in all of the patterns.

Several previous investigators have analyzed cichlid mating behavior in terms of Lorenz's releaser concept. It is felt that even in the expanded and modified form presented by Tinbergen, this concept is still too restricted to form an adequate basis for the analysis of *Tilapia* reproductive behavior.

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EXPLANATION OF THE PLATES.

PLATE I.

Fig. 1. Male cleaning nest. × .5

Fig. 2. Oviposition. The male is behind the female, waiting for her to move along so that he can pass over and fertilize the eggs. × .5

PLATE II.

Fig. 3. The male is fertilizing the eggs while the female is circling the nest. By the time fertilization was completed the female was directly behind the male, ready to lay a second round of eggs. × .5

Fig. 4. Male picking up the eggs. All of the eggs were gathered up in less than one minute. × .5

PLATE III.

Fig. 5. Male carrying eggs. × .7
(Photo. by S. C. Dunton, N. Y. Zool. Soc.).

Fig. 6. In special circumstances the female may carry the spawn. An egg can be seen at the tip of the open mouth of the female. × .5

ADDENDUM.

When this report was in page proof an article by Alfred Seitz (1948)—Vergleichende Verhaltensstudien an Buntbarschen (Cichlidae).—Zeitschrift für Tierpsychologie, *6* (22) : 202-235, was received from Germany. Here Seitz analyzes fighting and courtship behavior in two cichlid species, *Tilapia heudeloti* and *Tilapia natalensis*, in accordance with the theory of instinctive movements of Konrad Lorenz. On page 134 of the present paper we have noted the very close similarities of *T. heudeloti* and *T. macrocephala;* they may in fact be varieties or subspecies. However, the pictures of *T. heudeloti* presented by Seitz, the descriptions of the external morphology, particularly coloration, as well as the descriptions of courtship and fighting behavior, all suggest that he was dealing with a very different fish. It is not possible at this time to comment further on Seitz's paper, nor do we wish to venture any opinions concerning the complex problems of cichlid taxonomy, except to suggest to the reader who may wish to compare Seitz's paper with the present report that the *T. heudeloti* of Seitz and our *T. macrocephala* are perhaps very different species. —L.R.A.